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On the Occurrence of Protandric Hermaphroditism in the Mollusc Crepidula fornicata.

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(Communicated by Prof. Arthur Dendy, F.R.S. Received June 8,—Read June 24, 1909.)

Introduction.

Crepidula fornicata is a streptoneurous Gastropod belonging to the Calyptræidæ, a family of the Tænioglossa. It was first introduced into England from America about 1880 (1), when it was imported with American oysters. In America it is found on the east coast from Labrador to Florida, but in England so far as is known, it is confined to the Essex and Lincolnshire coasts, occurring, however, in abundance in shallow water in the neighbourhood of the mouths of the Crouch and Blackwater rivers. The conditions on the Essex coast seem to be highly favourable for its growth and propagation; indeed, so favourable, that within five or six years it has over-run the oyster beds at West Mersea. By attaching themselves very strongly to oyster-shells they cause the oyster fishermen much trouble, and it may be remarked, by competing for food and oxygen with the oysters may become a cause of much more serious trouble in the future. To obtain food the animals raise the anterior part of their shell, and extending the head to the front edge of the shell, move it slowly from side to side: at times the whole shell may be similarly turned slowly round to the one side or the other.

Crepidula fornicata is sedentary for the greater part of its life. It forms "chains," as Prof. Conklin calls them, by the curious habit the individuals have of fixing themselves in linear series one on the top of another as in fig. 1. Chains of as many as 12 individuals have been found. Viewed as a

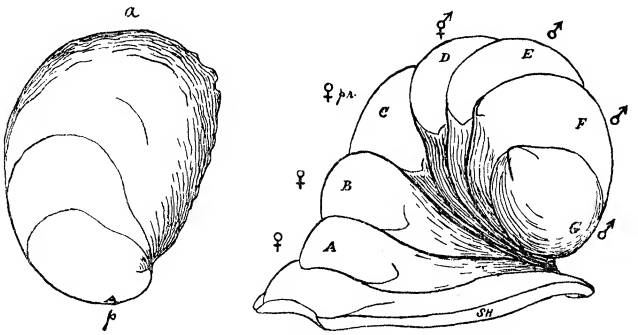

FIG. 1.—On the left; Dorsal View of a single Shell: *a*, anterior; *p*, posterior. On the right; a Postero-dextral View of a Chain attached to an Oyster-shell (SH). ($\frac{3}{4}$ nat. size.)

A, shell of proximal individual; B, shell of second individual, and so on. The symbols adjacent to the shells denote the secondary sexual characters of the inhabitants (see text).

whole, a chain is seen to form a spiral of about half a turn, bending over to the right.

On close examination of the chains it is found that when an individual settles down upon another it places the right antero-lateral border of its shell close to or touching that of the individual upon which it settles; since, however, the individual shells are roughly semi-ellipsoidal in shape, with the longitudinal axis a little concave to the right, and have the left side a little more convex dorso-ventrally than the right, it follows that the chain must form a right-handed spiral.

In a typical chain the twisting is accentuated by the gradual decrease observable in the size of the shells: the shell of the bottom or "proximal" individual being the largest, and that of the top or "distal" individual the smallest. The "proximal" individual always fixes the chain to some surface, as the shell of a dead or living animal, a pebble, or a piece of broken pot or glass. In America, chains of two or three individuals are found on the ventral surface of the King-crab (2, p. 10).

The following facts indicate that when a chain is once formed, none of the individuals separate:—

(1) The accurate fitting of each shell into the crevices and irregularities of the surface or shell upon which it occurs; hence, only short periods of separation of the individuals could be possible; no such periods have, however, been observed.

(2) In soft rock the proximal individuals wear a deep impression of the edge of the shell by the lateral movement executed in the search for food. In these cases the surface to which the middle of the foot is attached is not worn down, so that the animal becomes fixed on a boss of rock, which thus fits loosely into the aperture of the shell.

(3) Animals detached from a surface are apparently incapable of refixing themselves after a certain age, which I have not determined; for, immediately an animal is detached the sucker-like foot becomes "cupped" by a strong contraction of its muscle fibres; subsequent relaxation of the fibres does not seem to be possible.

(4) Prof. Conklin states that old individuals sometimes become permanently fixed by a calcareous secretion of the foot (2, p. 11).

There would seem to be no doubt, therefore, of the permanence of the chains. All the young ones, however, are motile, moving about by alternate extensions and contractions of the flat muscular foot.

Crepidula fornicata has hitherto been described as dicœcious, with a "marked sexual dimorphism" (2, p. 16), the males having been estimated by Prof. Conklin as being on the average three-quarters the size of the females. Those individuals were apparently called males, which had a muscular, cylindrical, and tapering outgrowth, the penis, on the right side of the head just behind the tentacle, as in fig. 2, ♂. Individuals having no

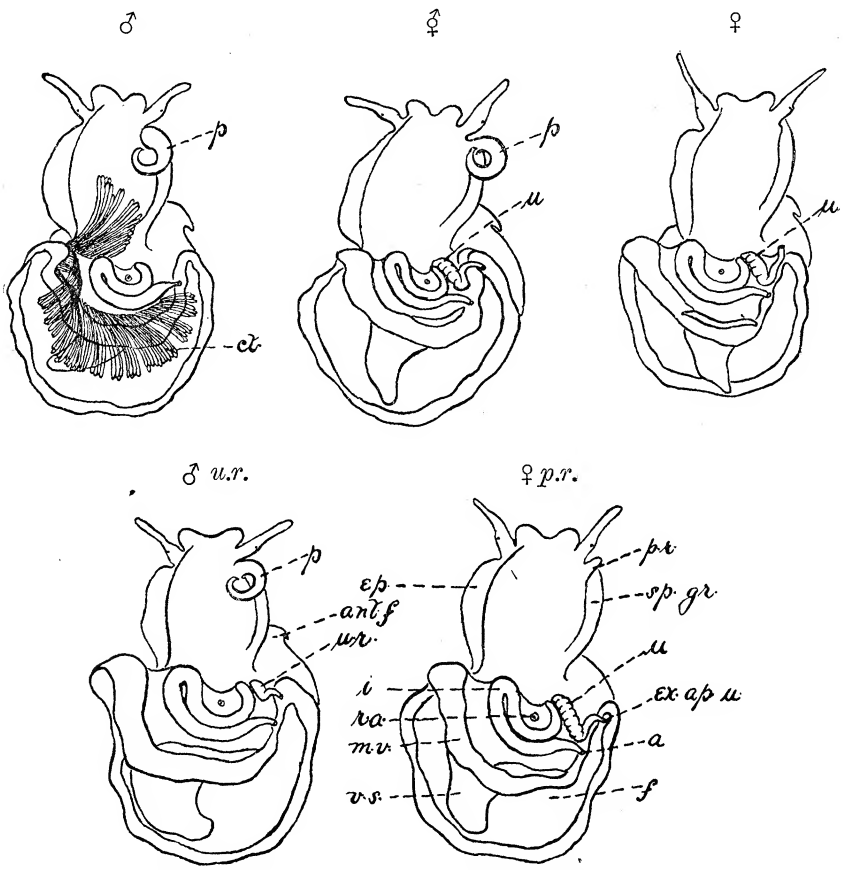

FIG. 2.—Illustrations of the Five Categories of Individuals in *C. fornicata*.

The animals were taken out of their shells and drawn from life (dorsal view), the mantle being turned back over the visceral sac. The branchial filaments are drawn only of the male. *p.*, penis; *u.*, uterus; *p.r.*, rudimentary penis; *u.r.*, rudimentary uterus; *a.*, anus: *ant.f.*, anterior part of foot; *c.t.*, branchial filaments; *ep.*, epipodium; *ex.ap.u.*, external aperture of uterus; *f.*, foot; *i.*, intestine; *m.v.*, mantle vessel; *r.a.*, external renal aperture; *sp.gr.*, sperm groove; *v.s.*, visceral sac. (Nat. size.)

such outgrowth on the head, but possessing a slightly spirally constricted tube, the uterus or external part of the oviduct, projecting on the right side of the mantle, were apparently called females (fig. 2, ♀). In dissecting a number of these animals I came across an hermaphrodite form, that is a form possessing both penis and uterus as in fig. 2 ⚥.

Before the commencement of this work, Prof. Dendy had kindly given me a large collection of the radulæ of *Crepidula fornicata* obtained by him at West Mersea, suggesting that I might investigate and compare the variability of the English and American stocks with respect to radular characters. I took the matter up, but after reading Prof. Conklin's work (2, pp. 19 to 25), on the genus Crepidula, decided to extend the investigation. Fresh material was obtained from West Mersea, and all of this was preserved in order to permit of correlation of all characters.

It was thought that the chain relations of individuals, and the sex relations in the chain would be interesting. A few *entire* chains were therefore preserved, and the relative position of the individuals recorded: thus the sex relations of the individuals in the chains were brought out as displayed in Table I.

Table I.

Ref. No.	A.	B.	C.	D.	E.	F.	G.	H.	I.
Chain 1	♀	♀	♀	♀	⚥	♂	♂	♂	♂ :
„ 2	♀	♀	♀	♂	♂	♂	♂ :		
„ 3	♀	♀	♀	♀	♀	⚥	♂	♂	♂ :
„ 4	♀	♀	♀	♂	⚥	♂ :			
„ 5	♀	♀	♂						
„ 6	♀	♀	lost	♂	♂	♂	♂ :		

In Table I the individuals in a chain are denoted by the letters, A, B, C, . . . etc., the proximal individuals being denoted by A, the next to the proximal by B, and so on. The chains therefore, read horizontally:—

Forms with a well-developed penis are represented by the symbol ♂
„ „ uterus „ „ ♀
„ „ penis and uterus „ ⚥

If the chains were found to be naturally complete,* two dots are placed after the last symbol, thus—♂ :

If the chain were doubtfully complete, one dot was placed similarly, thus—♂ ·

If the chain were known to be incomplete, only the symbol was used—♂

* Usually, in a naturally complete chain, the "distal" individual is a very young one. If, however, the distal individual is large, one can generally tell if it has had another individual on its back by the absence of the periostracum in an elliptical area on the right side of the shell.

A glance at the Table shows that all the individuals at the proximal ends of the chains are females, all the more distal individuals males, and those in the middle of the chain hermaphrodites. In discussing the records with Prof. Dendy, it occurred to us that the hermaphrodite condition appeared to be a stage in the life-history of all the individuals, and that as the males were the youngest, the hermaphroditism, if successive, must be protandric. Prof. Dendy suggested that an examination of young specimens would settle the matter. I immediately examined a collection of 48 young ones, and found them to be all males. Subsequently, 1000 young ones, namely, motile forms of the average size of about 1 cm., have been examined and found to be all males.* In a few cases the penis is a mere protuberance behind the tentacle, but as these are the smallest individuals—even larger ones requiring microscopical examination—they are doubtless the youngest males.

Sex Relations in the Chains.

A systematic examination of the sex relations of the individuals in the chains was begun at this stage. Observations of about 350 chains were recorded. A sample of the records made is shown in Table V (p. 476).

At the outset of the examination, however, it was found necessary to adopt additional categories to the ♂, ⚥, and ♀ ; for all stages were found on the one hand between ⚥ forms and ♂'s with a rudimentary uterus, and on the other hand between ⚥ forms and ♀'s with a rudimentary penis. The number of stages found, however, intermediate between ♂ and ⚥ was small compared with the number of stages found intermediate between ♀ and ⚥.

The following arbitrary categories were adopted :—

Males with a rudimentary uterus are represented by the symbol	♂ *u.r.* (= uterus rudimentary). See fig. 2, ♂ *u.r.*
Forms intermediate between ♂ *u.r.* and ⚥ are represented by the symbol	⚥ *u.s.* (= uterus small).
Females with a rudimentary penis are represented by the symbol	♀ *p.r.* (penis rudimentary). See fig. 2, ♀ *p.r.*
Forms intermediate between ⚥ and ♀ *p.r.* are represented by the symbol	⚥ *p.s.* (= penis small).
Occasionally individuals were found with both a small uterus and a small penis ; such are represented thus	⚥ *p.s.* (= penis small and uterus *u.s.* small).

In the records will be noticed here and there symbols which are bracketed, and another symbol or series of symbols placed alongside, and enclosed with

* As determined by the possession of a penis.

these in a square bracket, thus:—[(♂)(♂)♂]. This indicates that younger and smaller individuals settled down on members of the main or primary chain, and formed secondary or side-chains; occasionally even tertiary chains were found.

A comparison of the chains, even in Table V, brings out the regularity of the positions in which the different categories of individuals occur. As before, the ♀'s are found at the bottom of the chains, the ♂'s at the top, and the ⚥'s in the middle. Between the more distal ♀'s and the ⚥'s are found the ♀ *p.r.*'s; between the more proximal ♂'s and the ⚥'s or distal females are found the ♂ *u.r.*'s.

Hence, in a typical chain a series may be constructed to read from the top to the bottom, thus:—♂, ♂ *u.r.*, ⚥ *u.s.*, ⚥, ⚥ *p.s.*, ♀ *p.r.*, ♀.

It is interesting to note this series is just what one would expect to find if ♂'s passed successively through the different stages indicated, becoming finally ♀'s. It is certain, as will be shown later, that such a change does occur.

All lengths of chains occur from as many as 12 individuals in a chain down to one. A single individual was regarded as settled if its shell fitted accurately the irregularities of the surface upon which it was found, and if this surface were found to be clean. It is to be remembered that the records do not bring out the facts that in *all* chains there is typically a decrease in size from proximal to distal individuals.

In reviewing the records it is seen that a chain of a given length may be formed by various combinations of the five sex-forms (see chains 91, 338, 340, in Table V, p. 476), but the relative positions in the chains of individuals of the different categories are, with rare exceptions, constant. Occasionally it was found that an ⚥ form occurred between two ♂'s.

Chain Formation.

From a study of the records therefore, it would seem that chains are formed as follows:—

A male settles down on some surface, but before another male creeps on to its back it may pass through the series of changes from ♂ to ♀ as shown in Table II. Chains of one individual may be said to be at Stage I, chains of two individuals at Stage II, and so on.

At any time while the single male is changing into a female, another male might creep on to its back, settle down permanently, and form a Stage II chain. The new comer may then change to a female, and thus a Stage II chain might be found in any of the conditions represented in Table III. Similarly, another male might settle down upon a Stage II chain at any condition of the latter, and, changing in turn into a female, would form a

Stage III chain in one of the conditions represented in Table IV. Similarly, Stages IV and V, and so on, would be formed, and tables could be drawn up to indicate their different possible conditions.

Table II.*

	A.	B.	No of times found among records made.
Stage I (*a*) ...	♂ :		51
,, (*b*) ...	♂ *u.r.* :		0
,, (*c*) ...	♀♂ :		4
,, (*d*) ...	♀♀ *p.r.* :		11
,, (*e*) ...	♀		40

Table III.*

	A.	B.	C.	No. of times found among records made.
Stage II (*a*) ...	♂	♂ :		4
,, (*b*) ...	♂ *u.r.*	♂ :		1
,, (*c*) ...	♀♂	♂ :		3
,, (*d*) ...	♀♀ *p.r.*	♂ :		12
,, (*e*) ...	♀♀	♂ :		30
,, (*f*) ...	♀♀	♂ *u.r.* :		0
,, (*g*) ...	♀♀	♀♂ :		10
,, (*h*) ...	♀♀	♀♀ *p.r.* :		5
,, (*i*) ...	♀	♀ :		4

Table IV.*

	A.	B.	C.	D.	No. of times found among records made.
Stage III (*a*)	♂	♂	♂ :		0
,, (*b*)	♂ *u.r.*	♂	♂ :		0
,, (*c*)	♀♂	♂	♂ :		0
,, (*d*)	♀♀ *p.r.*	♂	♂ :		5
,, (*e*)	♀♀	♂	♂ :		11
,, (*f*)	♀♀	♂ *u.r.*	♂ :		1
,, (*g*)	♀♀	♀♂	♂ :		8
,, (*h*)	♀♀	♀♀ *p.r.*	♂ :		16
,, (*i*)	♀♀	♀♀	♂ :		5
,, (*j*)	♀♀	♀♀	♂ *u.r.* :		0
,, (*k*)	♀♀	♀♀	♀♂ :		3
,, (*l*)	♀♀	♀♀	♀♀ *p.r.* :		1
,, (*m*)	♀♀	♀♀	♀ :		1

* 1. In these tables the chains read horizontally and the life-histories of the individuals may be read vertically.

2. Some of these chains occur as side-chains.

On examining the whole of the records made of the natural chains, I find that all the conditions of chains shown in Tables II, III, and IV occur except Stage I (*b*), Stage II (*f*), and Stage III (*a*), (*b*), (*c*), and (*j*). The number of times each condition in these stages is found in the whole of the records is put in the right-hand column in Tables II, III, and IV. Probably the earlier conditions of Stage III chains do not occur because the ♂ period of life will already have been passed by "A" individuals before more than one or two males have been able to settle down on them. Since nearly all conditions

of Stages I, II, and III are found, I have no doubt that chains are formed as is indicated above. The relative frequencies of different lengths of chains in all the chains examined—including those in Table V—may be gathered from a glance at the curve in fig. 3.

From fig. 3 it is seen that the longer the chains are the less frequently do

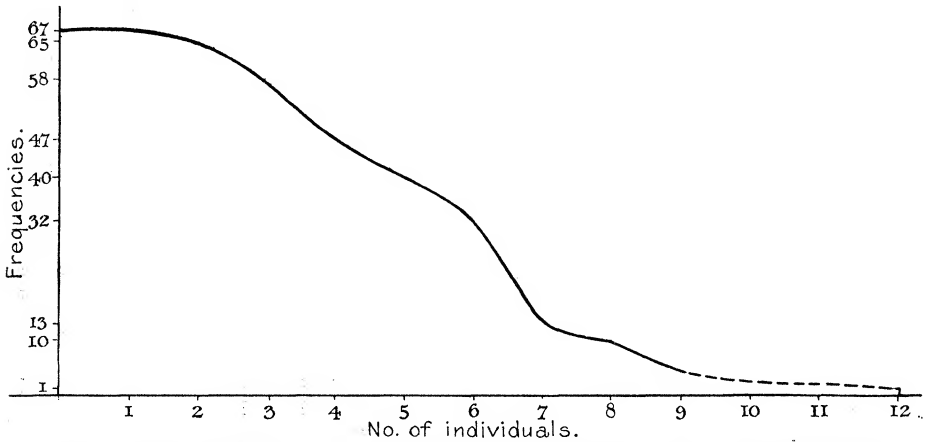

FIG. 3.—Curve showing frequencies of different lengths of chains among 336 chains. Ordinates = frequencies; abscissæ = individuals in chain.

they occur. Chains of 9, 10, and 11 individuals were not recorded once, and only one chain of 12 individuals was seen.

The age of change from ♂ to ♀, and the length of time required for the formation of a chain of given length are being investigated.

Some points in the records of the chains are noteworthy. The scarcity of ♂ *u.r.*'s is noticeable. Probably their rarity may be accounted for by the following facts.

(1) The uterus develops in the wall of the mantle, and is not visible externally until partly developed:* only those individuals were recorded as ♂ *u.r.*'s in which the end of the uterus projected from the mantle.

(2) The chains have only been examined between February and May this year: it is possible the change may occur rapidly at some other period of the year.

Single chains often afford evidence of the change from ♂ to ♀; such a series as ♀ *p.r.* ♀ *p.r.* ♀ is common; moreover, in these cases a gradual decrease in size of the penis from the ♀ to the proximal ♀ *p.r.* is also often observable; a point not brought out in the records.

* The development of the uterus is being investigated.

Table V.—Samples of the Records of the Sex Relations in the Chains of *Crepidula fornicata*.

Reference No. of chain.	A.	B.	C.	D.	E.	F.	G.	H.	I.	J.	K.	L.
80	♀	♀	♀	♂	♂	♂ :						
81	♀	♀	♂	♂	♂ :							
82	♀	♀ :										
83	♀	♀ *p.r.* ...	♂ :									
84	♀	♀	♀	♂ :								
85	♀	♀	♂	♂ :								
86	♀	♀ *p.s.* ...	♂	♂ :								
87	*?	♀	♂ :									
88	♀	♀ :										
89	♀	♀	♀ *p.s.*									
90	♀	♀	♀ :									
91	♀	♀	♂ :									
92	♀	♀	♂	♂	♂	♂ :						
93	♀	♀	♀	♀ *u.s.* ...	♂	♂	♂ :					
94	♀	♀	♀	♂	♂	♂	♂ :					
95	♀	♂ :										
96	♀	♀	♀	♂	♂	♂	♂ :					
97	♀	♀	♂	♂	♂ :							
98	♀	♀	♂	♂	♂ :							
99	♀	♀ ..... [(♀ *p.r.*) (A′♂) (A″ ♀ *p.r.*) (B′♂) (B″ ♀ *p.s.*) C′♂ C″ ♂]										
100	♀	♀	♀ *u.s.*	♂								
101	♀	♀ *p.r.* ...	♂ :									
102	*?	♀ [(♀ *p.r.*) ♀ *p.r.* ♂] ...	♀	♀ *p.r.* [(♀ *p.r.*) (♂) ♂]	♀ *p.r.* ...	♀ *p.r.* ...	♀ *p.s.* ...	♂ ...	♂ ...	♂ :		
103	♀	♀ ..... [(♀) ♀] ...	[(♀ *p.r.*) ♂]	♀ *p.r.* ...	♂	♂	♂ :					

320	♂ :								
321	♀ :								
322	♀ :								
323	♀ :								
324	♀ *p.r.* :								
325	♀ :								
326	♀ *p.r.* :								
327	♀ *p.r.* :								
328	♂ :								
329	♂ :								
330	♀ *p.r.* :								
331	♀ *p.r.* ...	♀ *p.r.* ...	♂ :						
332	♀ *p.r.* ...	♀ *p.r.* ...	♀ *p.r.* :						
333	♀ *p.r.* ...	♂	♂ :						
334	♀ *p.r.* ...	♂ :							
335	♀	♂ :							
336	*?	♀ *p.r.* ...	♀ *p.r.*.........	♀ *p.r.* ...	♀ *p.r.* ...	⚥ *p.s.* ...	♂	♂	♂ :
337	♀ *p.r.* ...	♀ *p.r.* ...	♂	♂					
338	♀ *p.r.* ...	♀ *p.r.* ...	♂	♂	♂ :				
339	♀	♀	♀ *p.r.* [(♀ *p.r.*)(♀)(♀ *p.r.*)♂]		♂	♂ *p.s.* :			
340	♀	♀	⚥ with eggs	♂ *u.r.* ...	♂ :				
341	♀	♀	♂	♂ :					
342	♀	♀ *p.r.* ...	♀ *p.r.*.........	⚥ *p.s.* ...	♂	♂ :			
343	♀	♂ *u.r.* ...	♂ :						

* The question marks indicate that only the shell was present, and that the chains, of which these are the first members, were found unattached to any foreign objects. It is therefore impossible to state whether the occupants of these shells were really the first members of the chains.

Relation of Primary to Secondary Sexual Characters.

Having established the fact that a completely continuous series in the reduction of the penis, and correlated increase in size of the uterus occurs, it became clear that continuity of the primary sexual characters should also be found. Accordingly, an investigation was made with this object in view, by means of serial sections of the gonad.

The gonad in all forms consists of two or three main tubes extending the whole length of the visceral mass, giving off tubular diverticula, which anteriorly divide and subdivide to form a loose compound tubular gland, but which posteriorly divide at most a few times, or are mere blind cæca. The cells lining the tubes proliferate, and some are shed into the lumina as germ cells—eggs or sperms.

In the male the main tubes of the gonad open into a vas deferens, from a dilatation of which a narrow tube leads to a groove on the dorsal surface of the body. This groove runs towards the head from the anterior end of the visceral sac to the base of the penis, and is continuous with a groove in the latter. In the female the main tubes of the gonad open into the oviduct. A receptaculum seminis opening into the oviduct has been described (3). The relation of the gonad to the gonaducts in the ♀ forms is being investigated. The colour of the gonad in the ♂ is brownish red, that of the ♀ brownish red or orange, occasionally yellow near the uterus, that of the ♀ yellow.

Sections of the ♀ forms were naturally cut first, but an examination of the gonad in all those investigated revealed nothing but ova. Sections of the "proximal" males were then prepared, with the result that both ova and sperms were found in the gonad. An examination of the gonad of all the males in a chain indicates, as far as observations go, that there is a gradual increase in ova in the gonad the nearer a male is to the most distal ♀ ; but even the smallest ♂'s examined have a few ova in their gonad.* It therefore seems doubtful whether pure males, *i.e.* males with only sperm in the gonad, are ever found in *Crepidula fornicata*. Hence the necessity of defining the term "male." The term "male" is usually applied to an organism which produces only sperm in its gonad. As, however, in most of the higher animals a special part of the body is modified into an intromittent organ, the presence of such an organ is adopted as a criterion of maleness. Usually this is a fair inference. In species presenting no sexual dimorphism, such as Amphioxus and Echinoderms, one resorts to the true criterion of maleness or femaleness, namely the production of ova or sperms in the gonad. In *Crepidula fornicata*, therefore, to be strictly accurate one should examine the gonad of every individual possessing even a well developed penis before committing oneself as to its sexual character. As a matter of convenience,

* Since G. Smith (4) has found ova in the gonad of the ♂'s of many species of Crustacea, it would seem that a careful microscopic examination of the gonads of all males, made in the light of these observations, might bring out important facts bearing on the nature of maleness.

however, I have adopted the simpler plan of calling all forms with a penis, males; it being understood that nothing more than the presence of the external male character is implied.

The youngest forms, however, are doubtless exclusively males as regards function, and the oldest forms probably exclusively females.

Examination of the gonad, then, at different periods in the life-history of *Crepidula fornicata*, makes clear that at first it produces ripe sperms only, but becoming with advancing age more and more egg-producing, until finally it is probably entirely egg-producing. There is, therefore, no doubt that all the individuals of this species are born as males, and change in the course of their life-history into females.

It is interesting to note that all stages of the gonad may occur among the individuals of a single chain. A comparison of the primary with the secondary sexual characters made at any phase in the life-history of an individual shows that the development of the former is always in advance of the latter; indeed, the primary sexual characters forecast the secondary sexual characters.*

It has been shown that the right antero-lateral borders of the shells of *all* the individuals in a chain are very close together; since the penis of the male and the external aperture of the uterus of the female are also on the right side anteriorly, it follows that any male in a chain could transfer sperms to any female; but no such transference has yet been observed.

Crepidula fornicata appears to be the only one of the many species of the genus which has taken to the habit of forming chains of more than two individuals;† in several other species, however, namely, *C. adunca*, *C. plana*, *C. convexa*, a male is often found mounted on a female (5). *Crepidula fornicata* is also the only species of the genus yet described as hermaphrodite, but probably other species are hermaphrodite, as will be shown below.

In *Crepidula fornicata* it would seem, therefore, that chain-formation and hermaphroditism are in some way causally connected. Knowing, as we do, that most of the genus Crepidula are sedentary in habit, and that sedentariness is associated throughout the whole animal kingdom with hermaphroditism; knowing, further, that a closely allied species, *Crepidula plana*, shows at least signs of, if not complete hermaphroditism (see below), it would seem that chain-formation is an adaptive phenomenon, which has arisen along with, and favoured the acquisition of, protandric hermaphroditism.

* In view of the conception of a sexual formative substance (4, p. 85), this phenomenon is not without significance.

† See footnote, page 482.

Chain-formation, along with protandric hermaphroditism, effects a strict economy of the sperm of the males, since the sperm is probably all transferred to the females; moreover, this arrangement probably ensures cross-fertilisation of *all* the females. In this respect chain-formation with protandric hermaphroditism is an advantage over permanent hermaphroditism with self-fertilisation, and no doubt leads to as great productiveness as would obtain in a motile unisexual condition. *Crepidula fornicata*, therefore, has become adapted to a sedentary life without losing any of the procreative advantages of a free-living habit.

The individuals forming side-chains are almost always on the left side of the primary chain, and therefore cut off from all sexual relations with any of the individuals of the latter. Here would appear at first sight to be a mal-adaptation, but individuals settling on a primary chain are quite comparable with those settling down on foreign objects; if the phenomenon is not due merely to chance, however, the former would appear to be the more gregarious.

Occurrence of Dwarf Females.

The variation in size in this species is indeed remarkable; it has been well described by Prof. Conklin (5, pp. 438 to 440). Size, besides being dependent on the usual conditions, is also determined by the extent of the surface of attachment. If individuals settle down on a small pebble or other surface where expansion is impossible, they remain permanently dwarfed. Mature dwarfed females have been found in such situations as small as 1·8 cm. long by 1 cm. wide, their shells being generally somewhat thickened, especially around the edge. On a flat surface of unlimited extent individuals may grow to a size of 5·5 cm. long by 3·5 cm. wide. *Crepidula fornicata* is thus able to regulate its shell-forming metabolic processes to the individual requirements. A similar readiness to adapt itself to its situation is exhibited by *C. plana*; but an even greater difference in the size of the extremes has been observed in this species by Prof. Conklin (2, p. 12), a race of dwarfs having been described by him as being one-thirteenth the size of the larger forms!

The smallest females found in *Crepidula fornicata* are the dwarfs mentioned above: they often occur in the middle of an oyster-shell surrounded by chains, the posterior ends of the shells of which converge on the *middle* of the oyster-shell, thus preventing expansion of the enclosed individual. Dwarf females, however, often have ♂ forms or ♀ *p.r.*'s fixed upon them, and since single settled males are found quite as small, there is no doubt that these small females have once been males and are really dwarfed. These dwarfs, as in the case of those of *C. plana*, appear to be dwarfs merely by

reason of their environment, being only, as Prof. Conklin provisionally calls them, "physiological varieties."

In some cases chains were observed in which the proximal individuals were more or less dwarfed, but as the posterior ends of the shells of dwarfs tend to overgrow the surface to which they are attached, especially if such be a small pebble, the dorsal surface of the shell of the proximal individual offers a larger surface than did the pebble, hence the "B" individuals in such chains are able to and do grow bigger than the "A" individuals. In such chains the largest individual is found about the middle, and is often an ♀ or even a ♂.

Chains dredged up just off the shore at West Mersea were found to consist of larger and more numerous individuals than those dredged up from "the Main," about 20 miles farther down the coast; these, however, may be phenomena arising from the usual conditions which determine size, as food supply, temperature of medium, chemical composition of medium, and so on.

Sex Phenomena in Allied Species.

Prof. Conklin has made estimations of the relative average volume of the ♂'s and ♀'s of several species of *Crepidula*, obtaining the following relations:—

The males of	*C. plana*	are	$\frac{1}{16}$	the size of	the females.
„	*C. adunca*	„	$\frac{1}{8}$	„	„
„	*C. convexa*	„	$\frac{1}{5}$	„	„
„	*C. fornicata*	„	$\frac{1}{4}$	„	„

He therefore naturally concludes that "There is then a marked sexual dimorphism in these molluscs, the mature females being generally much larger than the males; *the females are sedentary, the males locomotive* . . . . . " (2, p. 16).

In another place (5, p. 441) he further states: "In all species of *Crepidula* the males are smaller than the females . . . . " And again (5, p. 442) he states "That in the case of the other species named (*convexa, adunca, navicelloides, plana*) the males are never immovably fixed to one spot . . . , their shells also are not distorted so as to fit irregular surfaces as is the case with the females. In all cases locomotion is limited to small individuals. The young of all species and both sexes crawl about freely and rapidly. In *C. convexa* individuals of both sexes retain this power to a limited extent, *but the large females of adunca, navicelloides, and plana become firmly fixed, whereas the males of these species remain small and retain, to a certain extent, their power of locomotion** . . . . In *C. plana* the shell of the male is more nearly round than that of the female, and is usually more sharp-pointed at the apex . . . . [In a] number of individuals the older part of the shell has the male characters, while the newer part has those of the female.† "In

* The *italics* are mine.

† 2, p. 16.

such animals the penis is usually very small, and in some cases has almost entirely disappeared. Quite a complete series of stages in the degeneration of this organ was observed from the fully formed organ on the one hand to a minute papilla on the other. Sections of such animals show that neither male nor female sexual cells are produced at this time (!) The evidence seems to favour the view that we have in these cases an example of protandric hermaphroditism, but I am not able to assert that this is really the case, although I have spent much time in attempting to decide it."

From these quotations the following facts are brought to light:—

(1) The males in all species of *Crepidula* are smaller on the average than the females.

(2) The females of the species of *adunca*, *navicelloides*, and *plana* are fixed, but the males are motile.

(3) The adult females and males of *C. convexa* are motile to a limited extent.

In the light of the present observations on *Crepidula fornicata*, I have no hesitation in concluding that *C. plana* is also a protandric hermaphrodite, as Prof. Conklin suspected. It is highly probable also that the species, *adunca* and *navicelloides* are protandric hermaphrodites, but there is not sufficient evidence available for a judgment on *C. convexa*.*

A careful research on the proportions of the young males and females, and on the sexual character of the young of the various species of *Crepidula*, may bring out an interesting series of stages in the evolution of protandric hermaphroditism.

Sex Phenomena in the Streptoneura.

It is significant that Pelseneer should remark (6, p. 124) that "sedentary species (of Gastropods) often possess a rudimentary penis." Stimulated by this statement, I examined a collection of 160 *Calyptræa chinensis*, and found that *all* the small ones, about half the number examined, were ♂'s, while the larger ones were either ☿, ♀ *p.r.*, or ♀, but were nearly all ♀ *p.r.*'s. Since all the small ones are males, however, it would seem that this species is also a protandric hermaphrodite. An investigation is being made of the primary sexual characters to decide the question. It is probable, therefore,

* *July* 20.—Since the above was written, Mr. E. Smith has drawn my attention to a chain of *C. navicelloides* (probably ≡ *dilatata*), exhibited in the cases of the British Natural History Museum. I was kindly allowed to examine the Museum collection of Calyptræidæ, and in a collection of *C. dilatata* from Ancud I found the following chain—A, ♀ *p. r.*; B, ♂. In another collection of the same species from Patagonia, out of seven individuals the three smallest were ♂'s, the others being either ♀ *p.r.* or ♀. Thus stronger evidence is adduced for the above statements.

that protandric hermaphroditism may be found to be much more common in the Streptoneura than is thought at present. Pelseneer mentions 10 other Streptoneurous hermaphrodites, one of which, *Entoconcha*, is known to be protandric (6, p. 159); three others, *Entocolax*, *Entosiphon* (7), and *Exteroxenos* (8), are probably protandric. Six others occur, *Valvata*, *Bathysciadium*, *Odostomia*, *Cocculina*, *Oncidiopsis*, *Marsenina*, of which I have not found descriptions. *C. fornicata* may now be added to this list. Hence, it would appear that one of the chief distinctions between the Streptoneura and the Euthyneura is beginning to break down.

The sex phenomena observed in *Crepidula fornicata* support in a striking manner G. Smith's view (4, pp. 88, 89) of sedentarily-induced hermaphroditism, that is, suppression of females; moreover, the genus may be reasonably expected to offer stages in the evolution of this hermaphroditism, and so afford a means of testing the above-mentioned view. In the early stages of its evolution we should expect to find :—

1. A small percentage of young females among the spat.
2. Adult females of two kinds—

   (*a*) Those born as females.
   (*b*) Those born as males.

Recent Researches on Gametogenesis—besides the known fact that some Tænioglossa have two kinds of spermatozoa (6, p. 125)—give some hope that the two latter categories might be distinguishable by the cytological characters of their gametes.

Summary.

Crepidula fornicata is a Streptoneur of the family Calyptræidæ.

Individuals of this species associate permanently in linear series to form "chains." All lengths of chain composed of upwards to as many as 12 individuals have been found.

All the young are able to creep about, but the adults are sedentary.

The individuals in a chain offer a transitional series from maleness to femaleness both in primary and secondary sexual characters. Since all the young ones are males, the species is a protandric hermaphrodite.

Dwarf females occur as "physiological varieties."

Allied species and a species of an allied genus will very likely be shown to be protandric hermaphrodites.

There is good reason for thinking that this sex phenomenon may be even more widely spread in the Streptoneura.

Since the males in this species change into females, it would seem in this

case that it is the male which possesses the potentialities of both sexes. A solution to this problem is offered, if, as seems likely, allied species present an evolutionary series in the acquisition of protandric hermaphroditism.

I wish here to express my thanks to the College authorities for the facilities afforded me during the research. I am also deeply indebted to Prof. Dendy and Mr. Darbishire for important suggestions and valuable criticisms.

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